

The first report of the non-marine ostracod genus *Cavernocypris* Hartmann, 1964 (Crustacea, Ostracoda) from China, with a description of a new species

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Abstract

We describe *Cavernocypris xiangi* **sp. nov.**, the eighth nominated species of the genus, from two localities in Yunnan Province of southwestern China. As a member of *Cavernocypris* Hartmann, 1964, *C. xiangi* **sp. nov.** has short swimming setae on the second antenna, and its left valve overlaps the right valve on the ventral side. It can be distinguished from its congeners by the elongated, conspicuously pitted carapace and large lateral shield of the hemipenis. Along with two other yet unnamed species, we present the first reports of *Cavernocypris* from China and also the most southerly records of the genus worldwide, significantly expanding its known geographical range. Up to now, five of the eight named *Cavernocypris* species and the two unnamed members recovered in this study are restricted to East Asia, which could be a hotspot of diversity for the genus. The large morphological variation and the wide, patchy distribution of *Cavernocypris* imply that diversification in the genus has a long geological history.

Key Words

Cypridopsinae, groundwater, Fuxian Lake, taxonomy, zoogeography

Introduction

Yunnan Province, in southwestern China, stretches from the Qinghai–Tibetan Plateau in the north to the borders of Myanmar, Laos, and Vietnam in the south (Fig. 1). Consequently, it has an extensive elevation range (ca. 100–6750 m), providing many types of habitats, and is notable for its high levels of biodiversity and endemism in both terrestrial (Yang et al. 2004) and aquatic (Wiese et al. 2020; Chen et al. 2021) environments. In a checklist of non-marine ostracods from China, Yu et al. (2009) listed 42 species from Yunnan, mostly from Dianchi, Erhai and Fuxian lakes, and later works have increased this number (Yu et al. 2010; Liu and Xie 2014; Yu et al. 2022; Zhai et al. 2023). However, Zhai et al. (2023) noted that many of

these records are valves from lake sediments, and only 25 species can be confirmed as extant in the province. Ongoing surveys in Yunnan have revealed further species, including three belonging to the genus *Cavernocypris* Hartmann, 1964, the focus of this study.

Cavernocypris was erected to accommodate a Cypridopsinae species found in a cave in Afghanistan, *Cavernocypris lindbergi* Hartmann, 1964 (Hartmann 1964). This species was later synonymized with *Cavernocypris subterranea* (Wolf, 1920), which subsequently became the type species of the genus (Wouters 1983). Since then, a further five congeneric species have been described, one of which is subdivided into two subspecies, and an additional morphotype has been reported but not named (Hartmann 1964; McKenzie 1972; Marmonier et

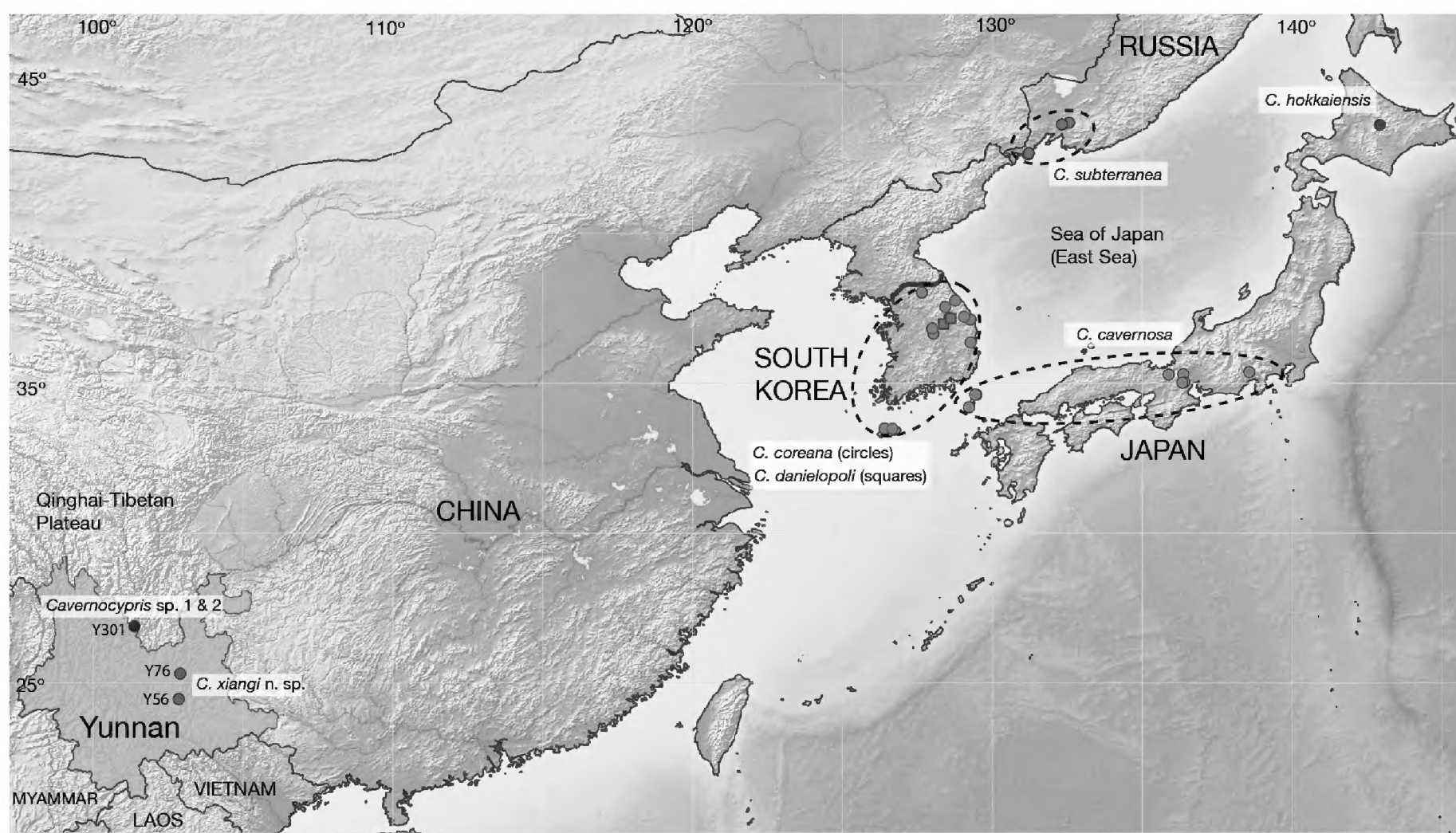


Figure 1. Distribution of *Cavernocypris* species in East Asia. Data from Chang et al. (2012), McKenzie (1972), Munakata et al. (2022), Schornikov and Trebukhova (2001), Smith (2011), Smith and Chang (2022), Smith et al. (2015, 2017), Tanaka et al. (2015), as well as the present study.

al. 1989; Smith 2011; Smith et al. 2017; Kulköylüoğlu 2020; Munakata et al. 2022). Species are typically found in habitats associated with groundwaters, such as springs, seeps, caves, and interstitial waters of riverbeds, although *C. subterranea* has also been reported from mountain lakes (see Meisch 2000 and Smith et al. 2017 for overviews). The genus is widely but sparsely distributed in North America and Eurasia, with the highest diversity in East Asia, where five species have been found in areas adjacent to the Sea of Japan (East Sea) (Fig. 1). However, there are no previous reports of this genus from China.

This study aims to describe and name one of three *Cavernocypris* species collected in Yunnan, with the other two left in open nomenclature due to insufficient numbers of specimens recovered. Figures of these latter two species are presented to provide additional information on the diversity and morphological variation within the genus.

Materials, methods, and terminology

Our new material of *Cavernocypris* Hartmann, 1964, was sampled from three sites in Yunnan (Fig. 1, Table 1). In the field, a net with 180 µm mesh and a metal handle was used to sieve the macrophytes and the bottom substrate, and the residue retained on the mesh was transferred to bottles and preserved in 70% ethanol. Electrical conductivity, temperature, and pH of the water were measured with a SANXIN PC5 device.

In the laboratory, the samples were transferred to a Petri dish, and the ostracods were picked under a JIANGNAN

SZ6000 stereomicroscope. The specimens were dissected with a pair of sharpened iron needles. The soft parts were sealed in Hydro-Matrix® (Dr. Richard Rudnicki, Micro Tech Lab, Austria) and examined with transmitted light microscopes (COIC BK3300 and Shang Guang XSP-12CA). Photographs of appendages, which were taken with a Canon EOS 5D Mark IV camera connected to an XSP-12CA transmitted light microscope, were traced in Microsoft PowerPoint 2019 to produce line drawings, with fine details at different focus horizons checked simultaneously under the microscope. The valves were imaged with an FEI QUANTA 650 scanning electron microscope after coating with gold. After analysis, these were kept dry in laser-cut micropalaeontological slides (PhD. Marian Golej, Kreativika Design, Slovakia). All specimens are housed in the Yunnan Key Laboratory for Palaeobiology, Institute of Palaeontology, Yunnan University, Kunming, China.

Geometric morphometric procedures were performed to detect the variation of valve outlines. For the present specimens, each valve was placed exterior-upwards on a glass slide and imaged under an XSP-12CA transmitted light microscope. Images of the same valve from different types of microscopes and different magnifications exhibit differences, albeit small (Suppl. material 1). Outlines digitized from lateral views of whole carapaces show larger dissimilarity compared with the single valves, probably because of the difficulties of placing carapaces exactly horizontally on the glass slide and/or identifying the margins of right and left valves accurately from the whole carapace (Suppl. material 2). As a result, to maintain the reproducibility of the data, we imaged single disarticulated

Table 1. Habitat information of *Cavernocypris* species from Yunnan Province, China, in this study. For abbreviations, see “Material, methods, and terminology.”

SN, date, and species	Habitat	Coordinates and altitude (m a.s.l.)	WD (m)	EC (μS cm ⁻¹)	T (°C)	pH	Substrate and vegetation	Specimens (* signifies male)
Y56-20200918, <i>Cavernocypris xiangi</i> sp. nov.	Littoral zone of Fuxian Lake	24°25'48"N, 102°50'58"E, 1720	0.3	na*	na*	na	Gravels covered with a few macrophytes and filamentous green algae	WOC164, WOC165*
Y76-20210805, <i>Cavernocypris xiangi</i> sp. nov.	Canal fed by spring	25°16'20"N, 102°52'51"E, 1973	0.5	335	14.0	7.55	Poorly sorted clastic material ranging from mud to gravels, with abundant emergent aquatic plants	WOC166*, WOC167*, WOC168, WOC169, WOC171, WOC172* (holotype), WOC173 (allotype), WOC175*
Y301-20230516, <i>Cavernocypris</i> sp. 1 and sp. 2	Slowly flowing river	26°48'20"N, 101°21'46"E, 1255	0.2	382	21.6	8.42	Gravels and mud, with macrophytes and filamentous green algae	<i>Cavernocypris</i> sp. 1: WOC193, WOC194 <i>Cavernocypris</i> sp. 2: WOC195

* These parameters were not measured for this particular site. According to the measurements at four other sites in the eastern and northern littoral zones of the lake on the same day, EC varied between 267 and 275 μS cm⁻¹, and T varied between 22.3 and 22.4 °C. We assume that the water parameters at the site Y56 were close to these values.

valves under the same magnification (200×) using the same microscope (XSP-12CA). Exterior views of single valves of *Cavernocypris* species figured in the literature, including Scanning Electron Microscope (SEM) images and line drawings, were digitized to obtain their outlines (Table 2). In a few exceptions when an exterior view of a valve was not available, interior views of valves and lateral views of carapaces were utilized.

The images of valves were digitized with the software TPSDIG2 (v. 2.31) (Rohlf and Bookstein 1990; Rohlf 2017). Each outline obtained was relocated [with the geometric centre at (0, 0)], rotated (with the antero-ventral and postero-ventral parts rested on the horizontal axis, cf. Danielopol et al. 2022, Fig. 3B), flipped (if necessary, to obtain the same orientation), and standardized for a surface area of 5000. A Fixed Outline Canberra Dissimilarity (FOCD) index was calculated to measure the dissimilarity between every two outlines (Wang et al. 2022). The computation and illustration of the outline data were made with the software Microsoft Office Excel 2019 and Microsoft Office PowerPoint 2019.

Abbreviations used in the text, figures, and tables. **A1**—antennule; **A2**—antenna; **Cp**—carapace; **dor.**—dorsal view/side; **EC**—electrical conductivity; **ext.**—exterior view/side; **GL**—genital lobe; **H**—height; **Hp**—hemipenis; **int.**—interior view/side; **L**—length; **ls**—lateral shield of Hp; **LV**—left valve; **L5/L6/L7**—fifth/sixth/seventh limb; **m a.s.l.**—meters above sea level; **Md**—mandible; **ms**—medial shield of Hp; **Mx**—maxillula; **na**—not available; **N**—number of values available for calculation; **RO**—Rome organ; **RV**—right valve; **SD**—standard deviation; **SN**—site number; **T**—temperature of water; **Ur**—uropod; **ven.**—ventral view/side; **W**—width; **WD**—water depth; **ZO**—Zenker organ. Terminology of the appendage chaetotaxy follows Broodbakker and Danielopol (1982), Martens (1987), and Meisch (2000). Numbering of the podomeres of the A1 follows an eight-segmented model (e.g., Smith and Kamiya 2007), which was slightly modified from Smith and Tsukagoshi (2005). Designations of Gm and GM claws of A2 follow fig. 2 of Martens (1987), fig. 6 of Meisch (2000), and Karanovic (2012, p. 26), with the more interior claw designated as GM and the more exterior one as Gm.

Results

Systematic description

Order Podocopida Sars, 1866
Superfamily Cypridoidea Baird, 1845
Family Cyprididae Baird, 1845
Subfamily Cypridopsinae Kaufmann, 1900
Tribe Cypridopsini Kaufmann, 1900

Genus *Cavernocypris* Hartmann, 1964

Type species. *Cavernocypris subterranea* (Wolf, 1920)
Diagnosis (amended from Smith et al. 2017). Cp shorter than 0.8 mm, elongated or triangular in lateral view, dorsal margin distinctly arched with or without hump on LV. LV larger than RV, overlapping right along ventral margin. Valve margins with peripheral selvage. Anterior, posterior, and ventral margins with well-developed fused zones with numerous and regularly placed marginal pore canals. Calcified inner lamella broad to very broad anteriorly and posteriorly. Inner list (sometimes weakly developed) on posterior areas of inner calcified lamella of one or both valves. Ventral margin of valves with or without outer lists. Surface of valves smooth or pitted. Swimming setae of A2 very short, scarcely extending beyond proximal margin of penultimate segment. Distal segment of Mx palp elongated, third endite (masticatory lobe) with two tooth-bristles. Respiratory plate of L5 reduced. L6 distinctly elongated. Seminiferous tubes of male simple loop (not spiral) in anterior part of Cp. Ur ramus tapering distally, not cylindrical.

Nominated species included. *Cavernocypris cavernosa* Smith, 2011; *Cavernocypris coreana* (McKenzie, 1972); *Cavernocypris danielopoli* Smith & Kamiya, 2017 in Smith et al. (2017); *Cavernocypris hokkaiensis* Munakata et al., 2022; *Cavernocypris reddelli* Külköylüoğlu, 2020; *Cavernocypris subterranea* (Wolf, 1920); *Cavernocypris wardi* Marmonier et al., 1989; and *Cavernocypris xiangi* sp. nov.

Table 2. Source of the published images used for outline digitization. For abbreviations, see “Material, methods, and terminology.”

Species	LV	RV
<i>Cavernocypris cavernosa</i> Smith, 2011	Smith (2011), fig. 1D, int.	Smith (2011), fig. 1B, ext. from Cp right view
<i>C. coreana elongata</i> (McKenzie, 1972)	Marmonier et al. (1989), figs 6A, 7B, ext.	Marmonier et al. (1989), figs 6B, 7A, ext.; Smith et al. (2017), fig. 6, ext. from Cp right view
<i>C. danielopoli</i> Smith & Kamiya, 2017 in Smith et al. (2017)	Smith et al. (2017), fig. 2A, ext. from Cp left view	Smith et al. (2017), fig. 2B, ext. from Cp right view
<i>C. hokkaiensis</i> Munakata et al., 2022	Munakata et al. (2022), fig. 2C, ext.	Munakata et al. (2022), fig. 2D, ext.
<i>C. reddelli</i> Külköylüoğlu, 2020	Külköylüoğlu (2020), fig. 2B, ext.	Külköylüoğlu (2020), fig. 2A, ext.
<i>C. subterranea</i> (Wolf, 1920)	Marmonier et al. (1989), fig. 3B, ext.; Fuhrmann (2012), tafel 117 1a, ext.	Marmonier et al. (1989), fig. 3A, ext.; Smith et al. (2017), fig. 6, ext. from Cp right view; Fuhrmann (2012), tafel 117 1c, ext.
<i>C. wardi</i> Marmonier et al., 1989	Marmonier et al. (1989), fig. 11A, ext.	Marmonier et al. (1989), fig. 11B, ext.
<i>Cavernocypris</i> sp. in Smith et al. (2017)	Smith et al. (2017), fig. 7A, ext. from Cp left view	Smith et al. (2017), fig. 7B, ext. from Cp right view

***Cavernocypris xiangi* sp. nov.**

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Figs 2–7

Type locality. Site Y76 (Fig. 1, Table 1), spring-fed canal in Fengze Botany Garden of Kunming, Yunnan Province, China (25°16'20"N, 102°52'51"E, altitude 1973 m).

Type material. All from type locality (Table 1). Holotype: dissected male (WOC172). Allotype: dissected female (WOC173). Paratypes: dissected males (WOC166, WOC167, WOC175) and females (WOC168, WOC169, WOC171). WOC166, WOC169, and WOC175 with valve articulation intentionally retained during dissection.

Other material examined. Dissected male (WOC165) and female (WOC164) from site Y56 (Table 1).

Derivation of name. Named after Ji Xiang (232–202 BC), a legendary military leader who rebelled against the cruel government of the Qin Dynasty in ancient China.

Dimensions. Male (n = 5) LV L 0.55–0.64 mm, H 0.28–0.33 mm, H/L 0.50–0.52 (Table 3). Female (n = 5) LV L 0.59–0.64 mm, H 0.30–0.34 mm, H/L 0.51–0.54. RV slightly shorter and lower than LV of the same individual and usually with smaller H/L. Cp (n = 2) W/L 0.46–0.48.

Diagnosis. *Cavernocypris* with elongated pitted Cp. Dorsal appearance of Cp relatively stout. Dorsal area of LV without hump. Antero- and postero-ventral calcified inner lamellae of LV with inner list. Valve morphology without obvious sexual dimorphism. LV exceeds RV along all margins and overlaps RV ventrally. Seta γ of Md palp smooth. Ventral-most seta on the same segment minute. Hp with wide and long ls significantly exceeding ms. Apical part of ls bluntly angular. ZO with 12–16 rosettes of spines.

Description. (Sex noted only when describing dimorphic features.) Cp and valves sub-reniform in lateral view (Fig. 2). LV larger than RV (Figs 2E, 3A) overlapping RV ventrally (Fig. 2G), resulting in less concave ventral margin than that of RV (Fig. 3B). LV and RV also with subtle differences in outline along anterior and posterior margins (Fig. 3B), with LV being less obtrusive at ventro-anterior and ventro-posterior areas but slightly less depleted at dorso-anterior and dorso-posterior areas. Sexual dimorphism in valve outlines subtle but persistent (Fig. 4). Both valves of female more obtrusive potero-ventrally but more depleted dorso-posteriorly and antero-ventrally (Fig. 4B, D). In other aspects, valve morphologies similar between

sexes and between RV and LV (Fig. 2). Highest point, i.e., antero-dorsal corner, at anterior 40–45%. Dorsal margin nearly straight, sloping posteriorly. Anterior margin broadly rounded. Posterior margin straight at upper section and narrowly rounded at postero-ventral corner. Ventral margin concave in RV, nearly straight in LV due to need to overlap RV (Fig. 3). Valve surface densely covered with pits that become smaller toward hinge area (Fig. 2F, I). Setal pores without rims. Selvage slightly displaced outwards at antero- and postero-ventral areas in both valves (Fig. 2A, C, H). In interior view, LV with inner list on both antero- and postero-ventral areas (Fig. 2D). RV with outer list easily observed from ventral view (Fig. 2G, J).

A1 (Fig. 5A) with eight segments, first and second fused into elongated base, supporting one dorsal seta and two sub-equal ventral setae. Third segment sub-quadrate, jointed with preceding and following segments, carrying one dorso-apical seta. Wouter’s organ and Rome organ possibly present but cannot be confirmed in present specimens. Fourth segment sub-trapezoidal, carrying one dorso-apical seta and one ventro-apical seta. Following segment boundaries without joint structures. Fifth segment sub-quadrate, with two long dorso-apical setae and two short ventro-apical setae. Sixth segment slightly elongated, with two long dorso-apical setae and two short ventro-apical setae. One of ventro-apical setae of this segment very short in some specimens (arrowed in Fig. 5A). Seventh segment elongated, with four long setae on interior surface and short seta α on dorso-apical position. Eighth segment slender, with three apical setae and aesthetasc ya. Aesthetasc ya more than three times length of this segment. Ventral seta slightly shorter than ya. Two medial setae much longer.

A2 (Fig. 5B–D) with two protopodal segments (coxa and basis), one exopodal segment, and three endopodal segments (penultimate segment undivided in both sexes). Coxa with two sub-equal ventro-medial setae. Posterior seta absent. Basis with one long ventro-apical seta. Small sclerotized patterns present on coxa and basis as arrowed in Fig. 5B. Exopodal plate small, carrying three setae, longest one reaching mid-way of penultimate segment. Third one sometimes cannot be seen. First endopodal segment carrying slender aesthetasc Y. Swimming setae short, with sixth (dorsal-most) one longest, extending to about mid-way of next segment. Ventro-apical seta extending to mid-way of claws. Second endopodal segment (penultimate segment)

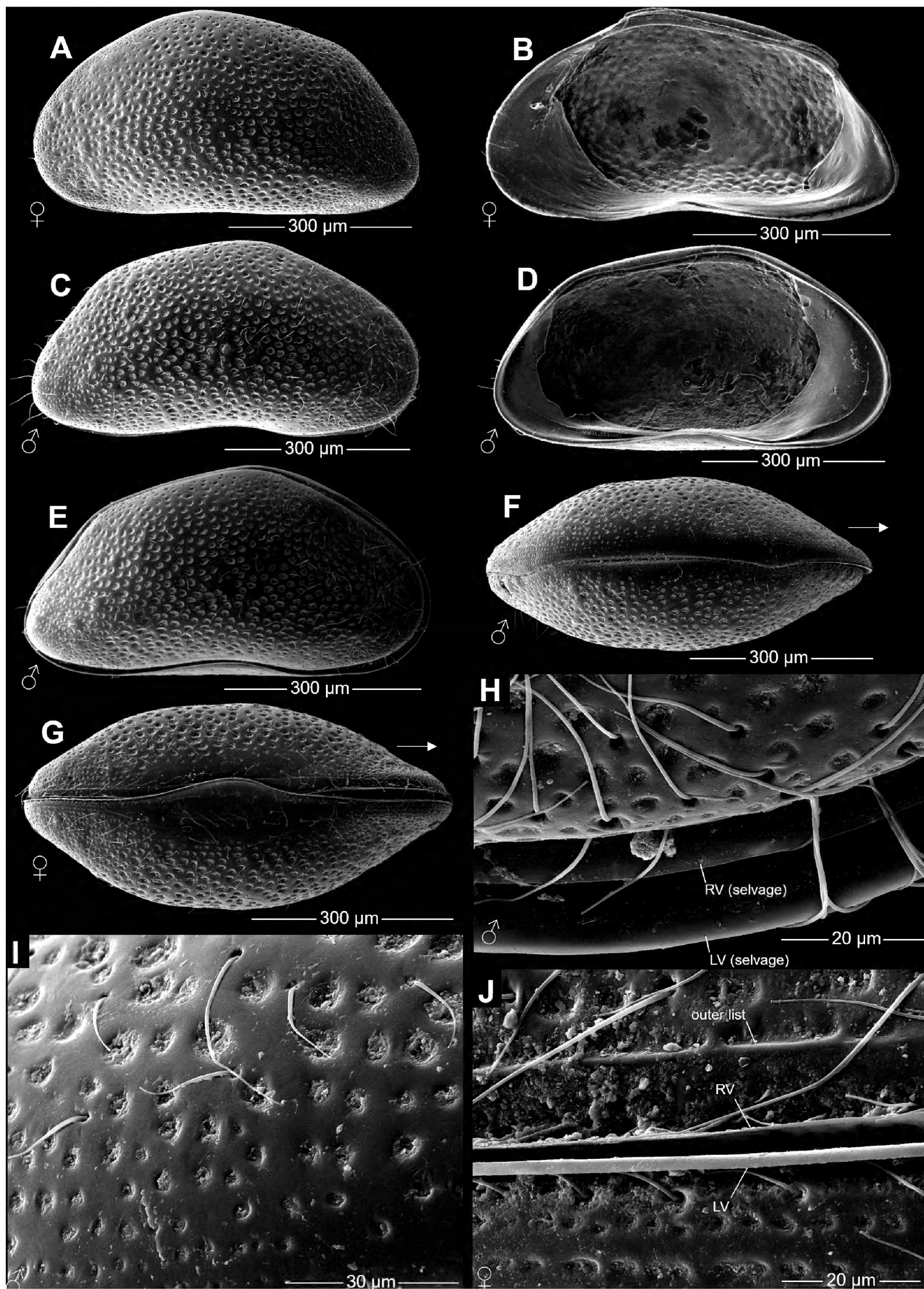


Figure 2. *Cavernocypris xiangi* sp. nov. **A.** LV, ext. (WOC173); **B.** RV, int. (WOC173); **C.** RV, ext. (WOC172, holotype); **D.** LV, int. (WOC172, holotype); **E.** Cp, right view (WOC175); **F.** Cp, dor. (WOC166). Arrow indicates anterior; **G.** Cp, ven. (WOC169). Arrow indicates anterior; **H.** Detail of antero-ventral margin of (E), showing details of the selvage. Note that the outer margin of LV is hidden beneath the selvage from this aspect; **I.** Detail of postero-dorsal part of LV of (F), showing decrease in pit size toward the hinge area; **J.** Detail of the potero-ventral part of (G), showing the outer list.

carrying minute y1 ventrally and two short, unequal setae dorso-medially. Female with 4 t-setae, t4 being shortest. Male with only 1 t-seta. Female z1–z3 all setae. Male z1 and z2 transformed into serrated claws, with z2 2/3 length of z1. Female G1–G3 all strong claws. Female G2 more strongly serrated than that of male. Male G1 and G3 both

setae extending to about mid-way of longest claws, G2 sub-equal to z1 in size. Female GM long serrated claw, Gm smooth claw, or strong seta extending to mid-way of GM. Male GM and Gm morphologies resembling female Gm and GM, respectively. Aesthetasc part of y3 extending to about mid-way of long claws in both sexes.

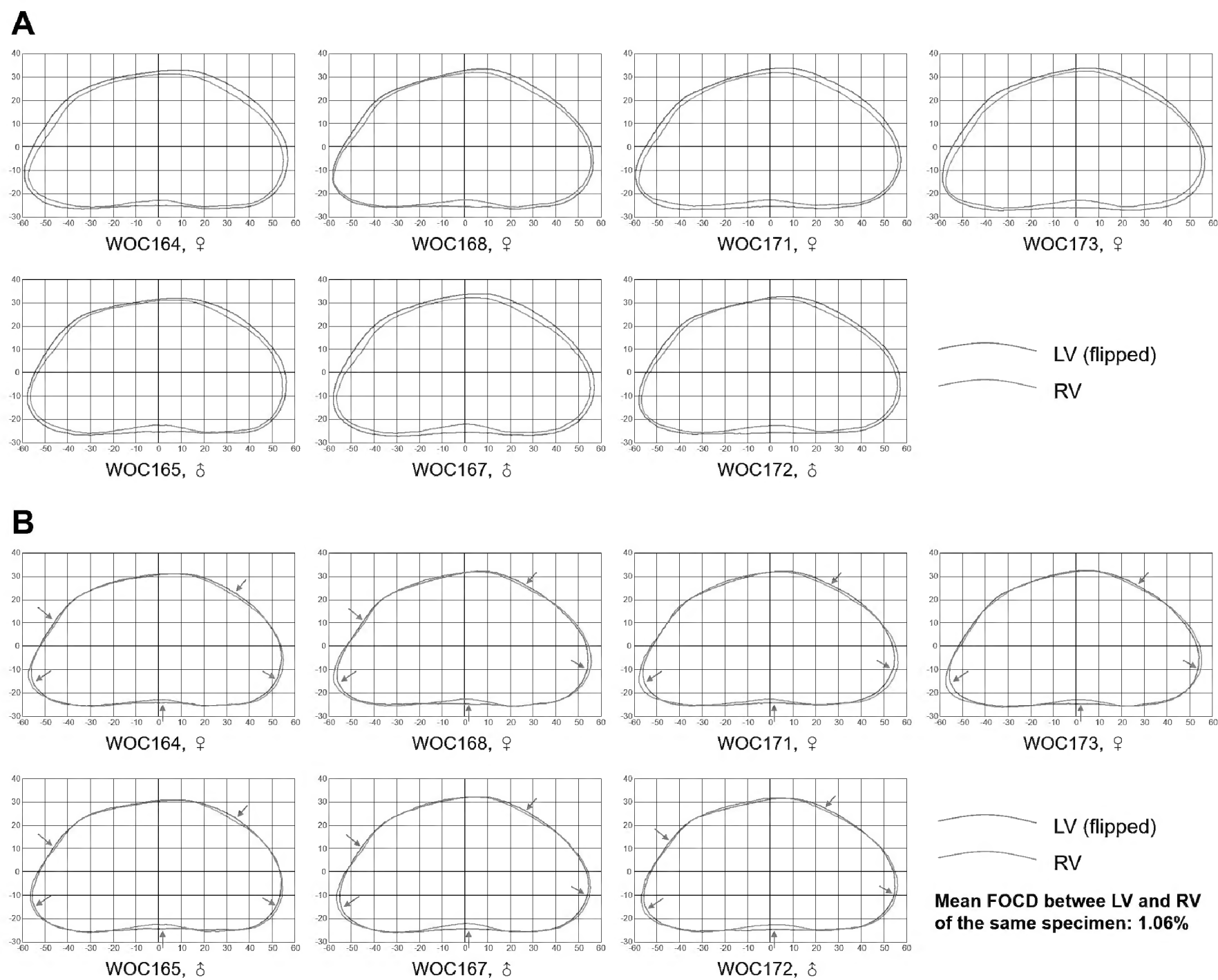


Figure 3. Comparison of the outlines of LV (flipped) and RV of the same specimen of *Cavernocypris xiangi* sp. nov. **A.** RV standardized to a surface area of 5000, LV in size relative to RV; **B.** Both valves of the same specimen standardized to a surface area of 5000. Blue arrows indicate the outline deviation of LV from RV. See Table 3 for basic parameters of the specimens.

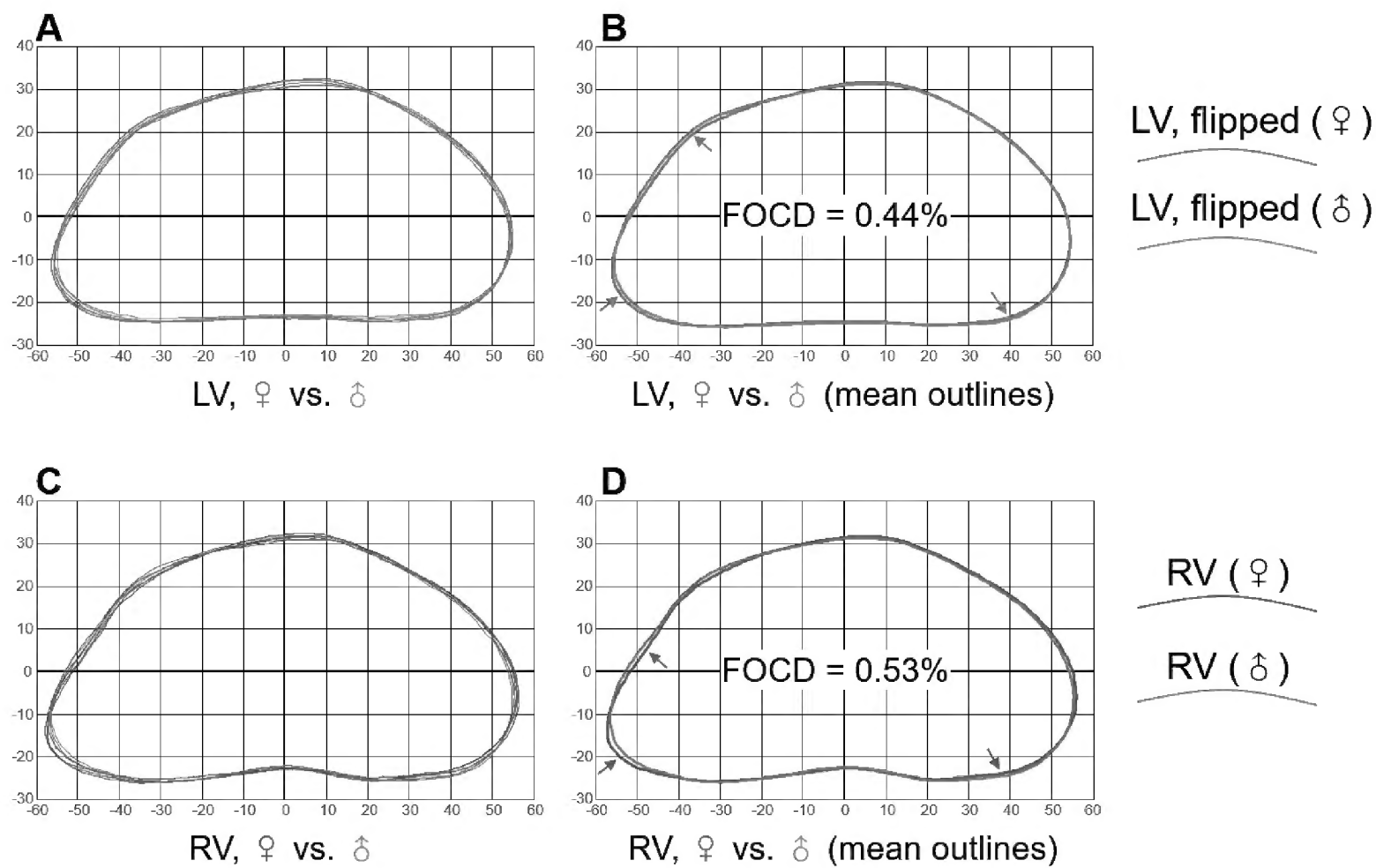


Figure 4. Comparison of the female and male outlines of *Cavernocypris xiangi* sp. nov. **A.** Four female LV and three male LV; **B.** Mean outlines of the female and male LV; **C.** Four female RV and three male RV; **D.** Mean outlines of the female and male RV. Blue and green arrows in (B) and (C) indicate the outline deviation of the female from that of the male. See Table 3 for basic parameters of the specimens.

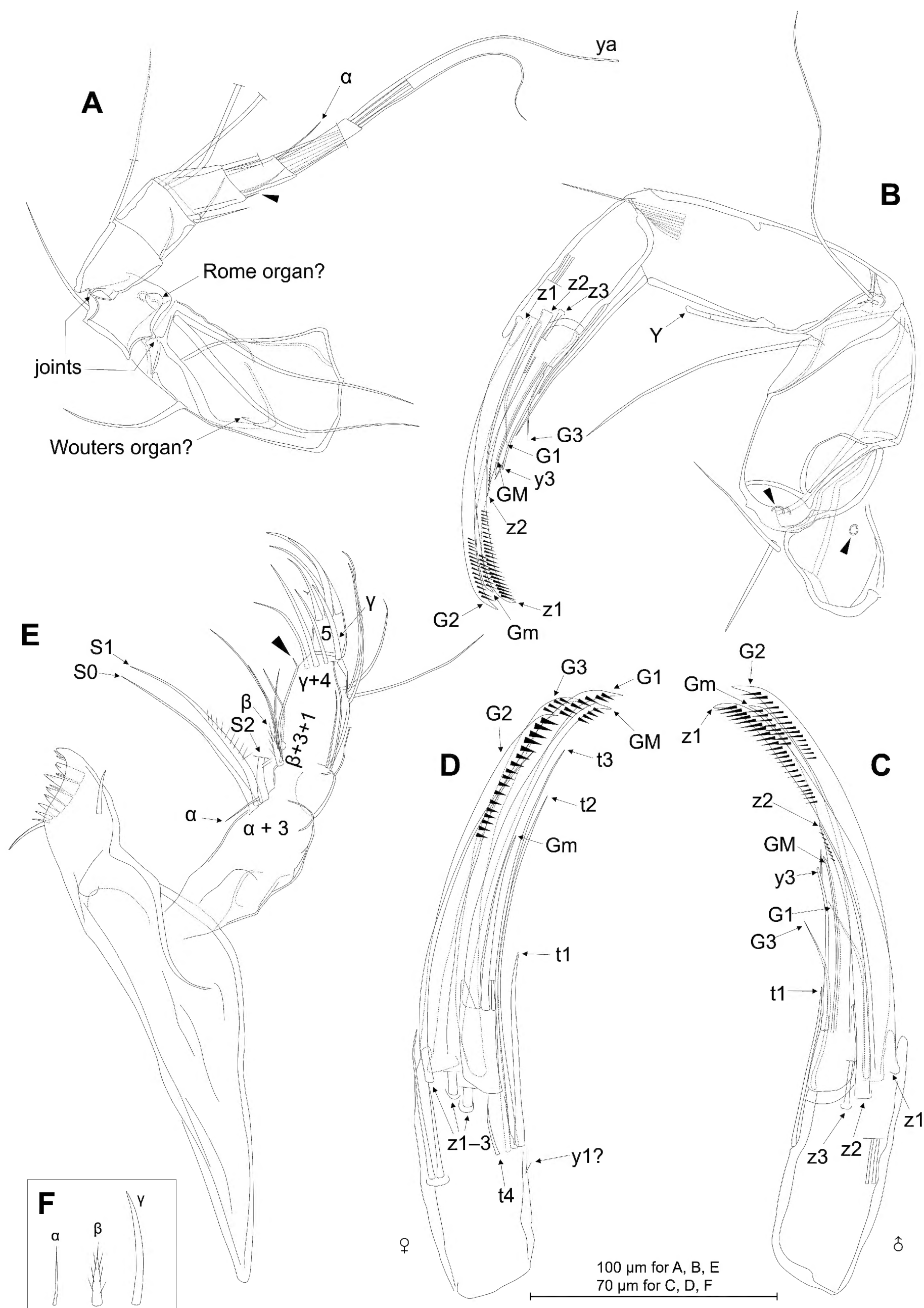


Figure 5. *Cavernocypris xiangi* sp. nov. **A.** A1 (WOC172, holotype). Arrowhead points to the minute ventral-most seta on the 6th podomere; **B.** Male A2 (WOC175). Small sclerotized patterns on coxa and basis arrowed. See text for detail; **C.** Distal part of male A2 of (B); **D.** Distal part of female A2 (WOC173). Note that G1 and G3 intersect at the middle part, so that the tip of G1 is situated to the ventral side of G3 (the basal part of G1 is situated to the dorsal side of G3); **E.** Md (WOC172, holotype), exopod not shown. Arrowhead points to the minute ventral-most seta on penultimate palp podomere; **F.** Setae α , β , and γ of (E).

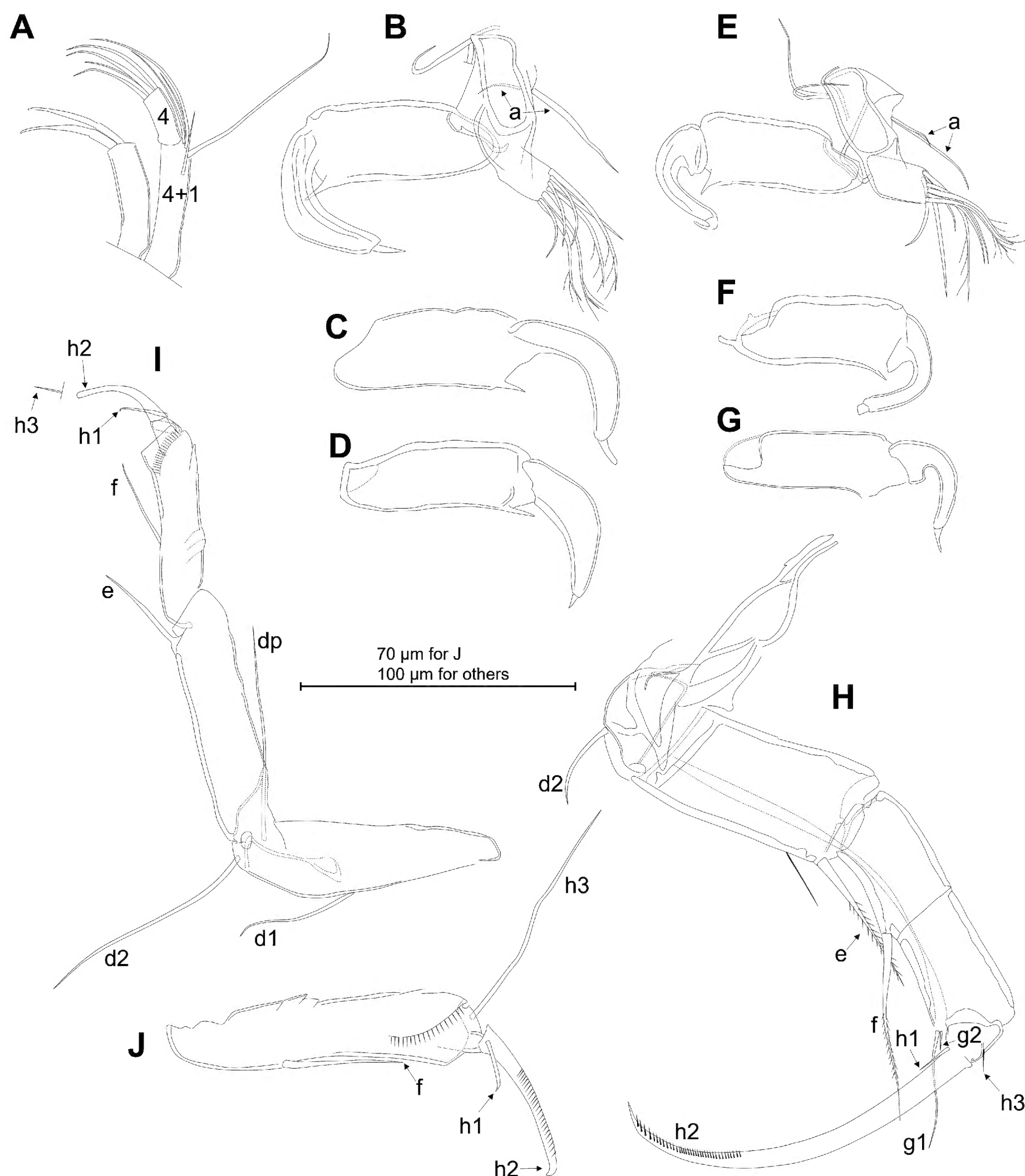


Figure 6. *Cavernocypris xiangi* sp. nov. **A.** Part of Mx, showing endopod and tooth-bristles on distal gnathobasic endite (WOC175). Numerals indicate numbers of setae on the first and second endopodal podomeres; **B–D.** Male right L5; **B.** WOC165; **C.** WOC175, protopod not shown; **D.** WOC167, protopod not shown; **E–G.** Male left L5; **E.** WOC165; **F.** WOC172 (holotype), protopod not shown; **G.** WOC175, protopod not shown; **H.** L6 (WOC172, holotype); **I.** L7 (WOC172, holotype); **J.** Distal part of L7 (WOC173).

Md (Fig. 5E, F) coxa elongated, endite distally with about 7 masticatory processes and with two unequal setae on inner edge and one short, stout, subapical seta near outer edge. Palp 4-segmented. First segment (basis) elongated, dorsally bearing exopod (not shown) with 1 short and 4 long rays, and ventrally with slender seta α and three long, thick setae. Second segment dorsally with three unequal thin setae and ventrally with thick plumose seta β , three smooth grouped setae, and one

longer smooth accompanying seta. Third segment dorso-subapically with four slender setae and apically with five setae, including thick smooth seta γ , three lateral setae, and one minute ventro-apical seta. Fourth segment with five claws/setae.

Mx palp (Fig. 6A) 2-segmented. First segment with one short sub-apical seta and four unequal dorso-apical setae. Second segment elongated, with four apical setae/claws. Tooth-bristles on distal gnathobasic endite smooth.

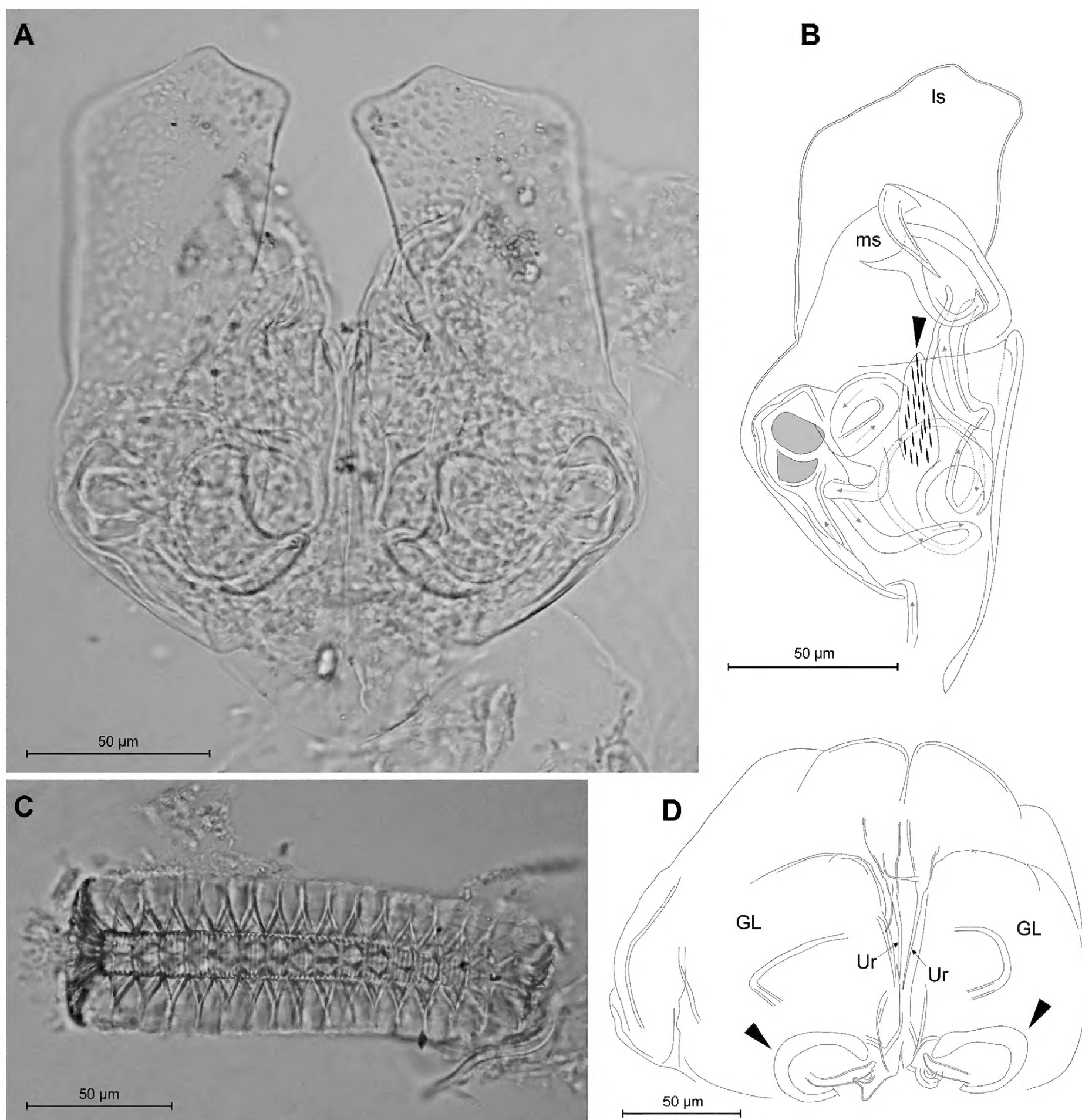


Figure 7. *Cavernocypris xiangi* sp. nov. **A.** Hp (WOC175); **B.** Hp (WOC172, holotype). Red arrows indicate pathways of sperms in the spermiduct. Black arrowhead indicates a spinous flap in Hp; **C.** ZO (WOC172, holotype); **D.** GL and Ur of female (WOC173). Arrowheads point to semi-circular tubes at the anterior area of GL.

Male right (Fig. 6B–D) and left (Fig. 6E–G) L5 palps unequal and with morphological variations between specimens. Trunk of right palp generally larger than that of left, both with small ventro-apical projection (projection in Fig. 6G lost, probably during preparation). Right clasper generally less curved than left, narrow (Fig. 6C) or comparatively wide (Fig. 6B, D). Distal end of claspers with small pointed sclerotized tip (blunt tip of Fig. 6F due to preservation or development). Protopod of L5 with comparatively long setae a (Fig. 6B, E). Setae b, c, and d absent. Exopod with two setae. Gnathobasic endite with about eight setae, some of which plumose.

L6 (Fig. 6H) with five segments. First segment (protopod) without seta d1, with well-developed d2. Second

segment (first endopodal segment) with plumose seta e. Anterior margin of this segment usually with 1–3 long pseudochaetae. Third segment stout, with plumose seta f. Fourth segment stout, with long, smooth seta g1 extending significantly beyond terminal segment and minute accompanying seta g2. Terminal segment short, carrying small seta h1, strong and distally serrated claw h2, and tiny seta h3.

L7 (Fig. 6I, J) first segment (protopod) with comparatively short setae d1 and sub-equally long setae d2 and dp. Second segment (first endopodal segment) with short seta e. Third segment with seta f protruding from mid-length and row of pseudochaetae in apical area. Distally with pincer arrangement, h2 relatively long.

Hp (Fig. 7A, B) elongated, with greatest width at about proximal 2/5. ls protruding significantly beyond ms, with bluntly angular end. ms tapering distally. Internal structures typical of Cypridopsinae. Labyrinth stout, accompanied by elongated spinous element (arrowed in Fig. 7B). Post-labyrinthal spermiduct with two full coils and descending tube.

Ur (Fig. 7D) present only in female, situated to interior side of GL. Basal part not cylindrical as in *Plesiocypridopsis* (cf. Meisch 2000), tapering distally. Two apical setae unequal.

GL (Fig. 7D) of each side consisting of two rounded lobes, broader anteriorly than posteriorly. Anterior part with semi-circular tube (arrowed in Fig. 7D). Medially lacking sclerotized hook/spine-like structure (e.g., those in *Plesiocypridopsis* and *Cypridopsis*).

ZO (Fig. 7C) elongated, with 12–16 rosettes of spines between two terminal plates. Central tube cylindrical, with fine transverse patterns.

Differential diagnosis. When males are present, *Cavernocypris xiangi* sp. nov. can be easily distinguished from congeneric species by the peculiar Hp that bears a large ls (Fig. 7A, B). Even if males are not available, the new species can be distinguished by the pitted valve surface and setal pores without rims (Fig. 2). The setal pores of at least *C. cavernosa*, *C. coreana*, *C. danielopoli*, and *C. subterranea* possess rims. *Cavernocypris hokkaiensis* has smooth valves, and the posterior valve margin is not as narrow as in *C. xiangi* sp. nov. The dorsal part of the valve of *C. reddelli* has only one apex (lacking a postero-dorsal angle) in lateral view, and its LV carries a prominent inner list in the posterior area. The swimming setae 1–5 on the A2 of *C. reddelli* are longer than seta 6, and its Hp (Külköylüoğlu 2020) resembles that of *Cypridopsis vidua* (Martens et al. 2023; Zhai et al. 2023), which belongs to another genus of the same tribe. These features make *C. reddelli* somewhat peculiar in the genus, and it can thus be distinguished from the new species. *Cavernocypris wardi* has serrated Mx tooth-bristles, and the proximal part of the Ur is much wider than that of the new species (Marmonier et al. 1989). The absence of setae b and d on the L5 of the new species makes it different from *C. coreana elongata* (seta b present, Marmonier et al. 1989; Külköylüoğlu and Vinyard 1998), *C. reddelli* (seta d present, Külköylüoğlu 2020), *C. subterranea* (both setae b and d present, Marmonier et al. 1989), *C. wardi* (both setae b and d present, Marmonier et al. 1989).

Cavernocypris sp. 1

Fig. 8A–D

Locality. Site Y301 (Fig. 1, Table 1), slowly flowing river in Huaping County.

Material examined. Two dissected females (WOC193 and WOC194).

Dimensions. Female LV (n = 2) L 0.59–0.61 mm, H 0.27–0.28 mm, H/L 0.47–0.48 (Table 3). RV (n = 2) L 0.57–0.60 mm, H 0.27–0.28 mm, H/L 0.47–0.48.

Brief description of Cp. Cp elongated in lateral view, with outline similar to those of *Cavernocypris xiangi* sp. nov. and *C. cavernosa* (Smith 2011), not triangular as in *C. danielopoli* (Smith et al. 2017). LV with ventral margin less concave than RV. Valve surface smooth. Setal pores with flat (not elevated) lip-like rims (Fig. 8D). In interior view, posterior calcified inner lamella of RV with selvage inwardly displaced (Fig. 8B, C).

Cavernocypris sp. 2

Fig. 8E–G

Locality. Site Y301 (Fig. 1, Table 1), slowly flowing river in Huaping County.

Material examined. One dissected female (WOC195).

Dimensions. Female LV (n = 1) L 0.66 mm, H 0.33 mm, H/L 0.50 (Table 3). RV (n = 1) L 0.64 mm, H 0.32 mm, H/L 0.50.

Brief description of Cp. Cp elongated in lateral view, similar to those of *Cavernocypris xiangi* sp. nov. LV with ventral margin less concave than RV. Valve surface rough, densely covered with small shallow pits and setal pores bearing elevated (volcano-like) rims (Fig. 8G). Calcified inner lamella of RV without inner list (Fig. 8F).

Variations in valve outline

There are currently two types of lateral outlines within the genus *Cavernocypris* (Fig. 9). *Cavernocypris danielopoli* and *Cavernocypris* sp. in Smith et al. (2017) (herein considered as a morphotype of *C. danielopoli*) exhibit a triangular outline, while all other species have elongated Cps with similar shapes in lateral view.

Cavernocypris xiangi sp. nov. belongs to the elongated-Cp group (Fig. 9). Although the shape differences between the RV and LV and between the two sexes are subtle, these can be detected by geometric morphometric analyses (Figs 3, 4, Table 4). As summarized in Table 4, the shape variation between valves from the same side (LV or RV) of the same sex (female or male) is on average 0.61%. The shape difference increases when valves from different sides (1.16%) or different sexes (0.69%) are compared and attains 1.27% when valves from different sides of different sexes are compared. The shape difference between the two valves of the same specimen averages 1.06%. The above data indicate that both right–left asymmetry and sexual dimorphism contribute to the valve shape variation of *C. xiangi* sp. nov., but sexual dimorphism plays a less significant role compared with asymmetry.

The geometric morphometric analysis can help distinguish between *C. xiangi* sp. nov. and its congeneric species. As shown in Table 5, when valves of the same side (either LV or RV) are compared, all other *Cavernocypris* species exhibit significant differences to *C. xiangi* sp. nov., with inter-species differences ranging from 1.07%

Table 3. Basic parameters of the specimens of *Cavernocypris* spp. from Yunnan used for geometric morphometric analysis. Disarticulated valves are used, and whole Cps are not used. All the valves were placed exterior-upwards and were measured under the 200× magnification of an XSP-12CA transmitted light microscope. For abbreviations see, “Material, methods, and terminology.”

Specimen and species	Sex	H/L of LV	H/L of RV	L_{LV}/L_{RV}	H_{LV}/H_{RV}
WOC164 (<i>Cavernocypris xiangi</i> sp. nov.)	♀	0.52	0.51	1.03	1.05
WOC168 (<i>Cavernocypris xiangi</i> sp. nov.)	♀	0.52	0.51	1.01	1.05
WOC171 (<i>Cavernocypris xiangi</i> sp. nov.)	♀	0.52	0.50	1.03	1.07
WOC173 (<i>Cavernocypris xiangi</i> sp. nov.)	♀	0.53	0.52	1.02	1.05
WOC165 (<i>Cavernocypris xiangi</i> sp. nov.)	♂	0.51	0.51	1.03	1.03
WOC167 (<i>Cavernocypris xiangi</i> sp. nov.)	♂	0.53	0.52	1.03	1.05
WOC172 (<i>Cavernocypris xiangi</i> sp. nov.)	♂	0.51	0.51	1.02	1.04
WOC193 (<i>Cavernocypris</i> sp. 1)	♀	0.47	0.46	1.04	1.04
WOC194 (<i>Cavernocypris</i> sp. 1)	♀	0.48	0.48	1.05	1.04
WOC195 (<i>Cavernocypris</i> sp. 2)	♀	0.50	0.49	1.04	1.06

Table 4. Intra-species variation of the valve outline of *Cavernocypris xiangi* sp. nov., measured as a Fixed Outline Canberra Dissimilarity (FOCD, %) index. All the valves were imaged for the exterior view under the 200× magnification of an XSP-12CA transmitted light microscope. SD, standard deviation; N, number of dissimilarity values used for calculation. For other abbreviations, see “Material, methods, and terminology.”

	Same sex, same valve	Same sex, different valves	Different sexes, same valve	Different sexes, different valves	Same specimen, different valves
FOCD (SD, N)	0.61 (0.12, 18)	1.16 (0.16, 25)	0.69 (0.19, 24)	1.27 (0.18, 24)	1.06 (0.15, 7)

Table 5. Valve outline dissimilarities between *Cavernocypris xiangi* sp. nov. and its congeners, measured as a Fixed Outline Canberra Dissimilarity (FOCD, %) index. Exterior views of disarticulated valves are compared, with a few exceptions. Comparisons are made between the same side valves, i.e., LV vs. LV and RV vs. RV. Note that the bottom row is the intra-species variation calculated from the FOCD values between the same side of valves in Table 4 (2nd and 4th columns therein). Abbreviations as in Table 4 and “Material, methods, and terminology.”

Species	FOCD (SD, N) with <i>Cavernocypris xiangi</i> sp. nov.
<i>C. cavernosa</i> Smith, 2011	1.21 (0.24, 14)
<i>C. coreana elongata</i> (McKenzie, 1972)	1.67 (0.42, 28)
<i>C. danielopoli</i> Smith & Kamiya, 2017 in Smith et al. (2017)	3.32 (0.68, 14)
<i>C. hokkaiensis</i> Munakata et al., 2022	1.08 (0.17, 14)
<i>C. reddelli</i> Külköylüoğlu, 2020	1.99 (0.25, 14)
<i>C. subterranea</i> (Wolf, 1920)	1.60 (0.70, 35)
<i>C. wardi</i> Marmonier et al., 1989	1.49 (0.35, 14)
<i>Cavernocypris</i> sp. in Smith et al. (2017)	2.69 (0.31, 14)
<i>Cavernocypris</i> sp. 1	2.30 (0.23, 28)
<i>Cavernocypris</i> sp. 2	1.07 (0.22, 14)
<i>Cavernocypris xiangi</i> sp. nov.	0.66 (0.16, 42)

to 3.32%, larger than the averaged intra-species difference of 0.66% for the latter (sex not discriminated due to minor sexual dimorphism described above). Among these, although *Cavernocypris* sp. 2 and *C. hokkaiensis* have small differences with *C. xiangi* sp. nov. in outline (FOCD values of 1.07% and 1.08%, respectively), valve ornamentation and the structures of the marginal zone (cf. Figs 2, 8, and fig. 2 of Munakata et al. 2022) can help further distinguish them.

Discussion

With the description of the new species herein, there are now eight named species in the genus *Cavernocypris* (cf. Meisch et al. 2019). The two yet unnamed species in our study indicate that the genus is more speciose. Additionally, Smith et al. (2017) noted significant variation in the height/length ratios of *C. subterranea* (ranging from 0.46 to 0.55), suggesting that there may be unrecognized diversity in the genus.

The genus *Cavernocypris* has a Holarctic distribution. Two species are found only in North America: *C. reddelli* and *C. wardi*. Another seven are restricted to East Asia: *C. cavernosa*, *C. coreana*, *C. danielopoli*, *C. hokkaiensis*, *C. xiangi* sp. nov., *Cavernocypris* sp. 1, and *Cavernocypris* sp. 2 (Fig. 1). *Cavernocypris subterranea*, on the other hand, has a distribution in both North America and Eurasia (including western Eurasia and East Asia). There are five species in areas adjacent to the Sea of Japan (East Sea), in Japan, Korea, and the Far East of Russia (Fig. 1). Based on these data, a possible scenario is that East Asia is the center of diversity for this genus. The new records of *Cavernocypris* herein are the first from China and the most southerly records known, although they were found at relatively high altitudes (1255–1973 m, Table 1) under a temperate climate. The Chinese records are several thousand kilometers from previous records, east or west, suggesting that the distribution of the genus may be far wider than currently known.

Cavernocypris species are typically found in habitats associated with groundwaters, including springs, seeps, caves, and interstitial waters of rivers and streams (Smith et al. 2017). *Cavernocypris subterranea* has also been reported from mountain lakes, but probably in association with underwater springs (Meisch 2000). *Cavernocypris xiangi* sp. nov. was recovered from two habitats in our study, the littoral zone of Lake Fuxian (Y56) and a canal fed by a spring (Y76, the type locality) (Fig. 1, Table 1). The first habitat is unusual for the genus in that it is not obviously connected to groundwaters, although we cannot rule out underwater springs flowing into the lake at the collection site. The other two species, *Cavernocypris* sp. 1 and *Cavernocypris* sp. 2, were both recovered from a slowly flowing river (Y301, Fig. 1, Table 1), again not obviously connected to groundwater, but they may be representatives of interstitial populations in the riverbed.

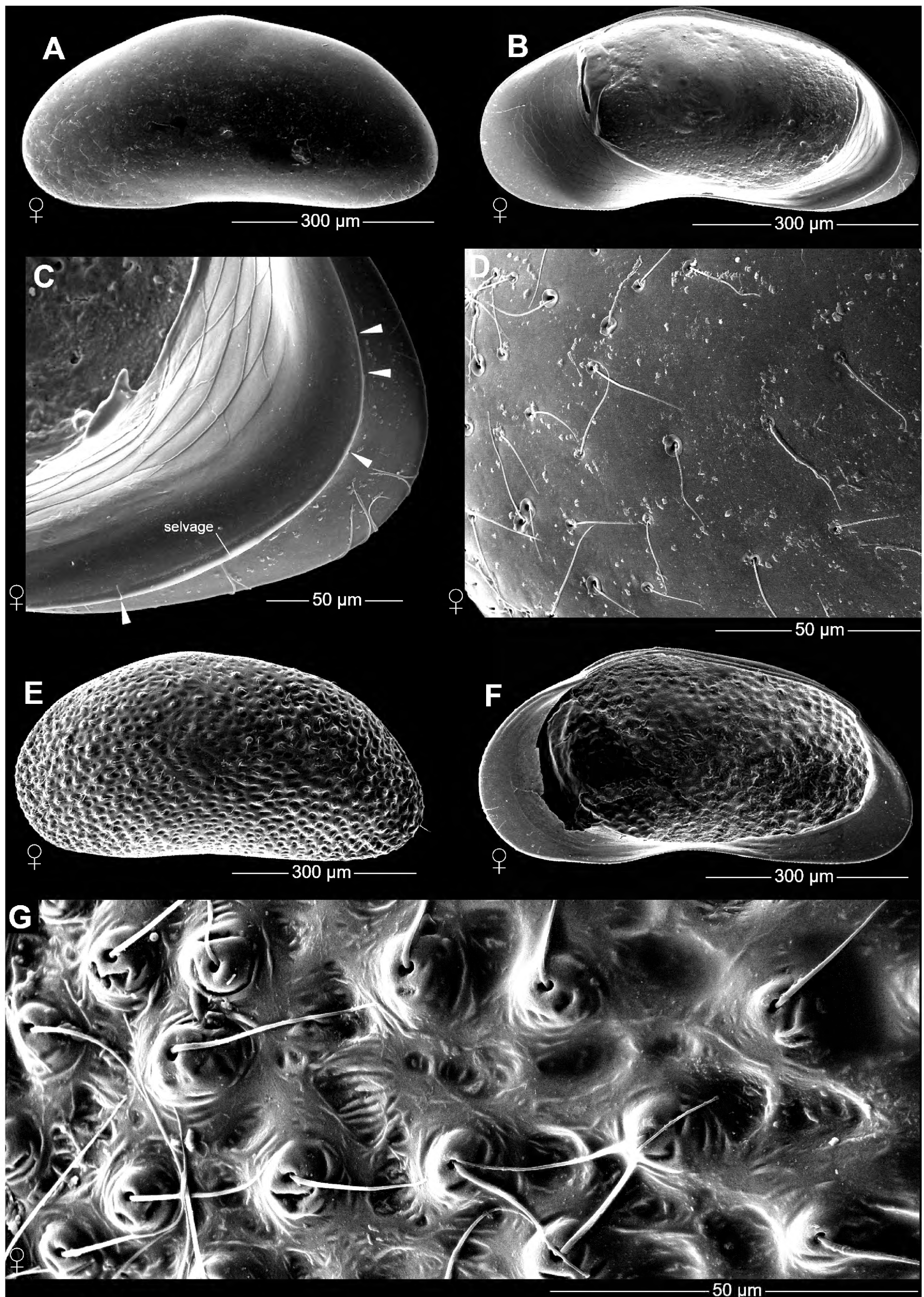


Figure 8. *Cavernocypris* sp. 1 (A–D, WOC193) and *Cavernocypris* sp. 2 (E–G, WOC195). **A.** LV, ext; **B.** RV, int; **C.** Detail of postero-ventral part of (B), showing the displaced selvage and the reticulation on the calcified inner lamella. Arrowheads point to setal pores along the selvage; **D.** Detail of the surface of (A); **E.** LV, ext; **F.** RV, int; **G.** Detail of the surface of (E).

Cp ornamentation in *Cavernocypris* is interspecifically variable, with species strongly pitted all over (*C. cavernosa*, *C. xiangi* sp. nov., *Cavernocypris* sp. 2), lightly pitted in the central to posterior areas (*C. coreana*, *C. danielopoli*, *C. subterranea*), or entirely smooth (*C. hokkaiensis*, *C. wardi*, *Cavernocypris* sp. 1). Meanwhile, intraspecific variation of Cp ornamentation also occurs. For example, although *C. subterranea* generally has a central band of pits, entirely smooth examples have been reported (Marmonier et al. 1989). Cp ornamentation may not always have phylogenetic significance and instead can be examples of homoeomorphy related to water chemistry. Reeves et al. (2007) noted that subterranean Candonidae in the Pilbara region of Australia differ in shape and ornamentation, with smooth, tapered forms (of *Areacandona* and *Deminutiocandona*) found in alluvial aquifers, large, well-calcified forms (of *Humphreyscandona*) in bicarbonate waters, and ornate forms (of *Meridiescandona*) in Mg^{2+} -rich, lower pH environments. Limited details of water chemistry are available for two sites in this study (Table 1), but the smooth *Cavernocypris* sp. 1 and the highly ornate *Cavernocypris*

sp. 2 were found in the same sample, suggesting that in this case, water chemistry is not influencing Cp ornamentation.

The genus has a mixture of sexual, asexual, and mixed reproduction. Males were first reported for the genus in both subspecies of *C. coreana* (McKenzie 1972), although later all-female populations of *C. coreana elongata* were found in surface habitats, indicating mixed reproduction (Chang et al. 2012). *Cavernocypris subterranea* in Eurasia consists of all-female populations, but males have been reported from one site in North America, suggesting geographical parthenogenesis for this species (Külköylüoğlu and Vinyard 1998). The North American *C. reddelli* is currently only known from the type locality, but males are present (Külköylüoğlu 2020). *Cavernocypris wardi*, *C. cavernosa*, *C. danielopoli*, and *C. hokkaiensis* are all only known as female populations. Thus, *C. xiangi* sp. nov. is the fourth species of the genus for which males are known.

There is noticeable morphological variation in the shapes of both the lateral and medial shields of the hemipenes between species (Fig. 10). Other notable morphological variations in the genus include Cp structure,

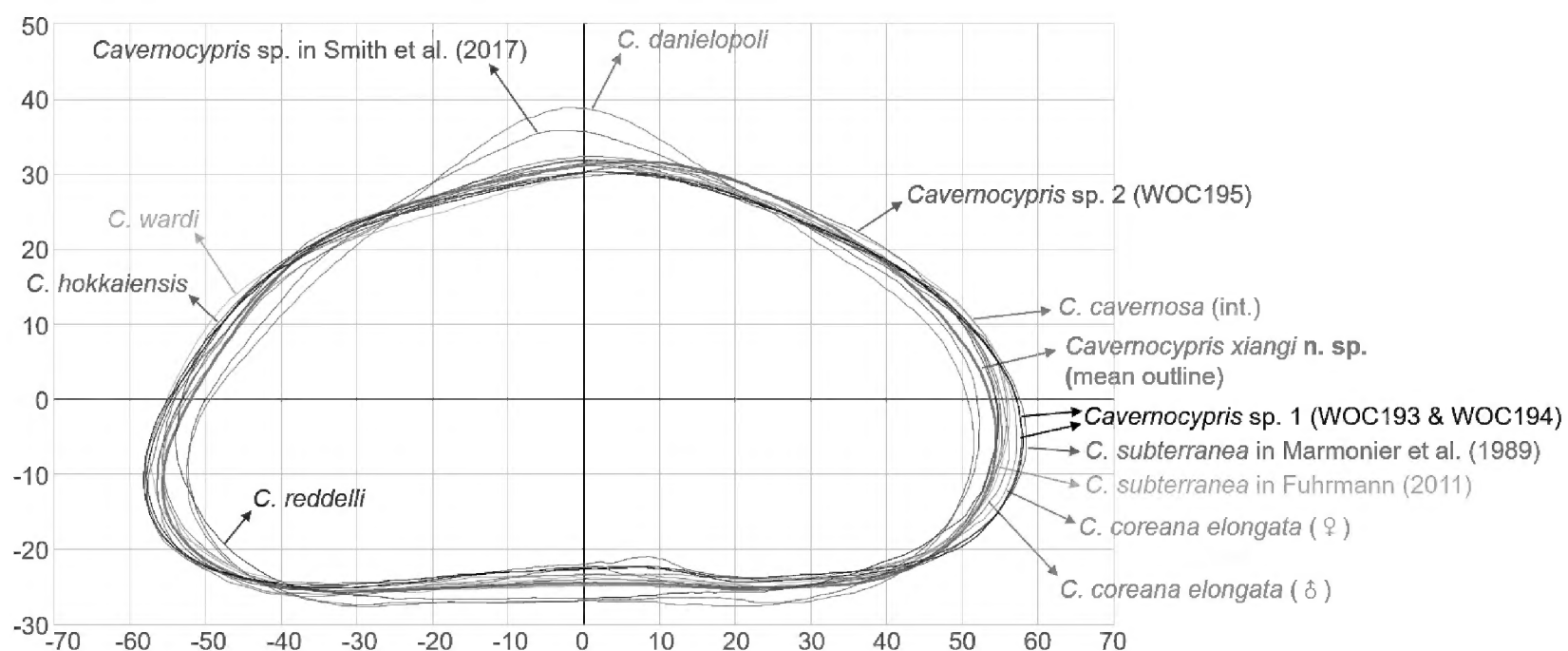


Figure 9. Comparison of the outlines of different species of *Cavernocypris*, represented by exterior views of LV (except *C. cavernosa*, for which the interior view is used). All the valve outlines are standardized for a surface area of 5000.

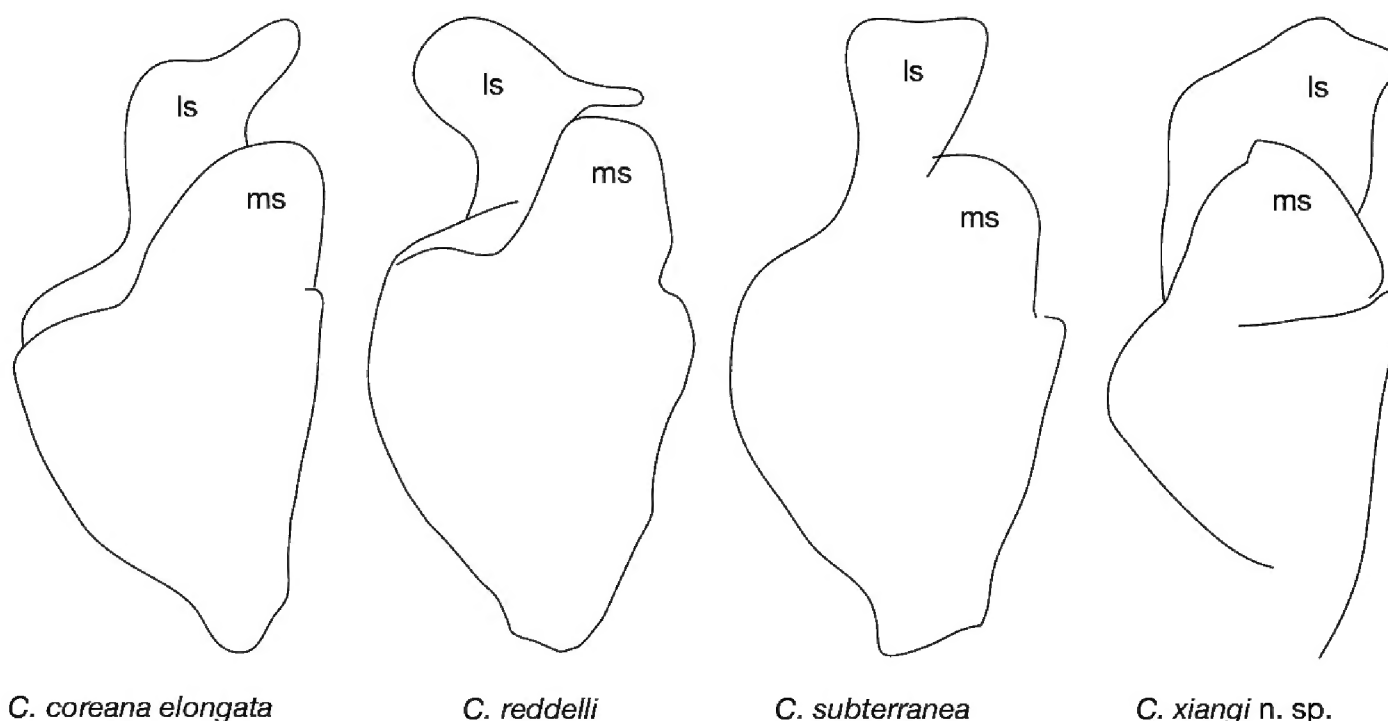


Figure 10. Outlines of the hemipenes of *Cavernocypris* species. Modified from Marmonier et al. (1989), Külköylüoğlu and Vinyard (1998), Külköylüoğlu (2020), and this study. *Cavernocypris subterranea* and *C. reddelli* inverted to aid comparisons. ls = lateral shield, ms = medial shield.

number of segments in the antennule, and setal arrangements of fifth limbs (see table 2 of Munakata et al. 2022 and above), features often used to discriminate genera rather than species. The genus also has a wide but patchy distribution (see above), unusual for groundwater genera, which tend to be endemic to relatively small areas (Karanovic 2007). This large morphological variation, together with the wide, patchy distribution, suggests that diversification in the genus occurred a long time ago or that the genus contains different evolutionary lineages with convergent morphologies, e.g., the reduced swimming setae. Phylogenetic analyses based on morphological and/or molecular features could test if the genus is monophyletic or contains examples of homoeomorphy, common in subterranean ostracods (e.g., Hotèkpo et al. 2024).

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Supplementary material 1

Dissimilarity of the outline of the same valves of *Cavernocypris xiangi* sp. nov.

Authors: Dayou Zhai, Robin J. Smith, Dongdong Zhang

Data type: xlsx

Explanation note: Dissimilarity of the outline of the same valves of *Cavernocypris xiangi* sp. nov. photographed under different settings (dark blue and light blue areas), in comparison with other intra-species dissimilarity values.

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Link: <https://doi.org/10.3897/zse.101.141525.suppl1>

Supplementary material 2

Dissimilarity of the outline sampled from lateral views of carapaces to disarticulated valves (yellow numerals in green area), in comparison with other intra-species dissimilarity values

Authors: Dayou Zhai, Robin J. Smith, Dongdong Zhang

Data type: xlsx

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